

# CONTRIBUTIONS TO THE REPRODUCTIVE BIOLOGY OF *PANAX TRIFOLIUM* L. (ARALIACEAE)<sup>1</sup>

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**Abstract:** Flowering phenology, pollination, and morphological aspects of pollen and seeds of *Panax trifolium* L. are investigated. Plants are apparently androdioecious, but with very minor differences in pollen between floral forms (staminate and hemaphrodite). Light microscope and SEM studies were made of pollen and seeds.

*Panax trifolium* L. (Dwarf ginseng) is a springtime herb of eastern North America which perennates as a bulbous underground rhizome in moist forested areas. The genus is also represented in the region by the more economically important *Panax quinquefolium*. However, the latter is much less common due to over-collection for its reputed medicinal purposes.

There is relatively little information available concerning the biology of either species of *Panax*. What is available deals largely with *P. quinquefolium*<sup>2</sup> and is derived mostly from cultivated material, rarely from plants in their natural habitat (Hu, et al., 1980). Hu, et al. discussed the general ecology and habitat of both species but pointed out the lack of information concerning their growth habit, population structure and longevity of individuals. There are also few published reports for either species concerning field observations on flowering phenologies, breeding systems, and pollination.

Morphologically *Panax trifolium* is polygamous, with staminate and hermaphroditic flowers occurring on separate plants. The function of the gynoecium in the staminate flower is seldom questioned due to its very reduced nature; it completely lacks an ovary. However, the functionality of the pollen in the seed-producing hermaphroditic flowers is not as apparent and has not been investigated. A result of this lack of understanding is illustrated by the varied descriptions of sexual condition in the literature; "mostly unisexual" (Hu, et al., 1980), "dioeciously polygamous" (Fernald, 1950), and "often unisexual" (Gleason & Cronquist, 1963).

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<sup>2</sup>While this paper was in press another article dealing with *Panax quinquefolium* was published: Lewis, W. H., & V. E. Zenger. 1982. Population dynamics of the American Ginseng *Panax quinquefolium* (Araliaceae). *Amer. J. Bot.* **69**: 1483-1490.

The purpose of this paper is to report on investigations of several aspects of the reproductive biology of *Panax trifolium*. These include flowering phenologies, pollination, and morphological aspects of pollen and seeds. The results of these investigations suggest that *Panax trifolium* is androdioecious, a very uncommon and hence very interesting form of polygamy in which staminate and hermaphroditic flowers occur on separate plants (Lloyd, 1975; Charlesworth & Charlesworth, 1978).

#### MATERIALS AND METHODS

This study is based primarily on observations of two populations of *Panax trifolium* located in Durham, New Hampshire. For flowering phenologies 15 staminate and 15 hermaphroditic plants were selected, labelled with colored threads, and numbered. Each of these plants was then visited daily from 27 April to 4 June, 1981. Fruit development was subsequently followed in the same manner.

Observations of pollinators were made during the above visits to the populations. Floral insect visitors were collected by applying fine strands of Tanglefoot (The Tanglefoot Co., Grand Rapids, Michigan) to inflorescences of 10 plants of each type. The trapped insects were then collected the next day and preserved in 95% ethyl alcohol for later identification.

Pollinator exclusion experiments were conducted by covering 15 hermaphroditic plants with nylon screening before the flowers matured. The screens were removed after the flowering period and possible fruit development observed.

For pollen morphology studies, material was collected from both populations, acetolyzed (after Faegri & Iversen, 1975), rinsed twice with distilled water, and transferred to glycerine jelly. Microscope slides were then prepared from this material for light microscope (LM) observations. For scanning electron microscope (SEM) observations acetolyzed pollen was washed in two rinses of 100% acetone and transferred to aluminum stubs. The mounted material was then coated with approximately 200 angstroms of paladium gold.

Seeds were collected from each population for morphological studies. Observations were made of air dried seeds with a binocular dissecting microscope. For SEM observations air dried seeds were mounted on aluminum stubs using double-stick tape and coated

with palladium gold. All SEM observations were made on an AMR 1000 Scanning Electron microscope at the University of New Hampshire.

Descriptions of pollen and seeds are based on LM observations with supplemental information from SEM micrographs. All data in this study were evaluated statistically using an analysis of variance, or in the case of P/E ratios (pollen morphology), a Mann-Whitney U-test.

The amount of pollen produced per anther was estimated by counting all the grains in one sac and multiplying by two, pollen:ovule ratios were then calculated. Pollen was stained on glass microscope slides by dissecting open anthers in a drop of the respective stain (Aniline blue, Aceto-carmin, and Malachite green-acid fuchsin). Cover glasses were then applied and observations made by examining most grains on the slide.

Investigations of herbarium material were made in three herbaria; Hodgdon Herbarium, University of New Hampshire (NHA), The New England Botanical Club Herbarium (NEBC) and the Gray Herbarium (GH) at Harvard University. Observations were made by examining each reproductive specimen and noting the sexual makeup of the inflorescence.

#### POLLEN MORPHOLOGY

Pollen grains of *Panax trifolium* are radially symmetrical, isopolar and tricolporoidate, with three long, narrow colpi reaching nearly to the poles. The poroid areas are formed by a distinct zone of nexine thickening which incompletely surrounds a thinner area in the equatorial region of the colpus (Fig. 2, D,E). The regions of thickening form two separate semi-circular areas on opposite sides of the thin area and aligned parallel to the equatorial axis (Fig. 3, E). The poroid areas are approximately 4 to 5  $\mu\text{m}$  in width, measured along the polar axis, and 5 to 6  $\mu\text{m}$  in length, measured along the equatorial axis. The nexine is also thickened along the margins of the colpi (Fig. 2, G; Fig. 3, A), thus forming a margo that is apparent when the grain is expanded but is less distinguishable when the colpi are invaginated.

In cross section the tectate exine is composed of two distinct zones; the inner nexine and outer sexine (Fig. 2, C; Fig. 3, A, B).

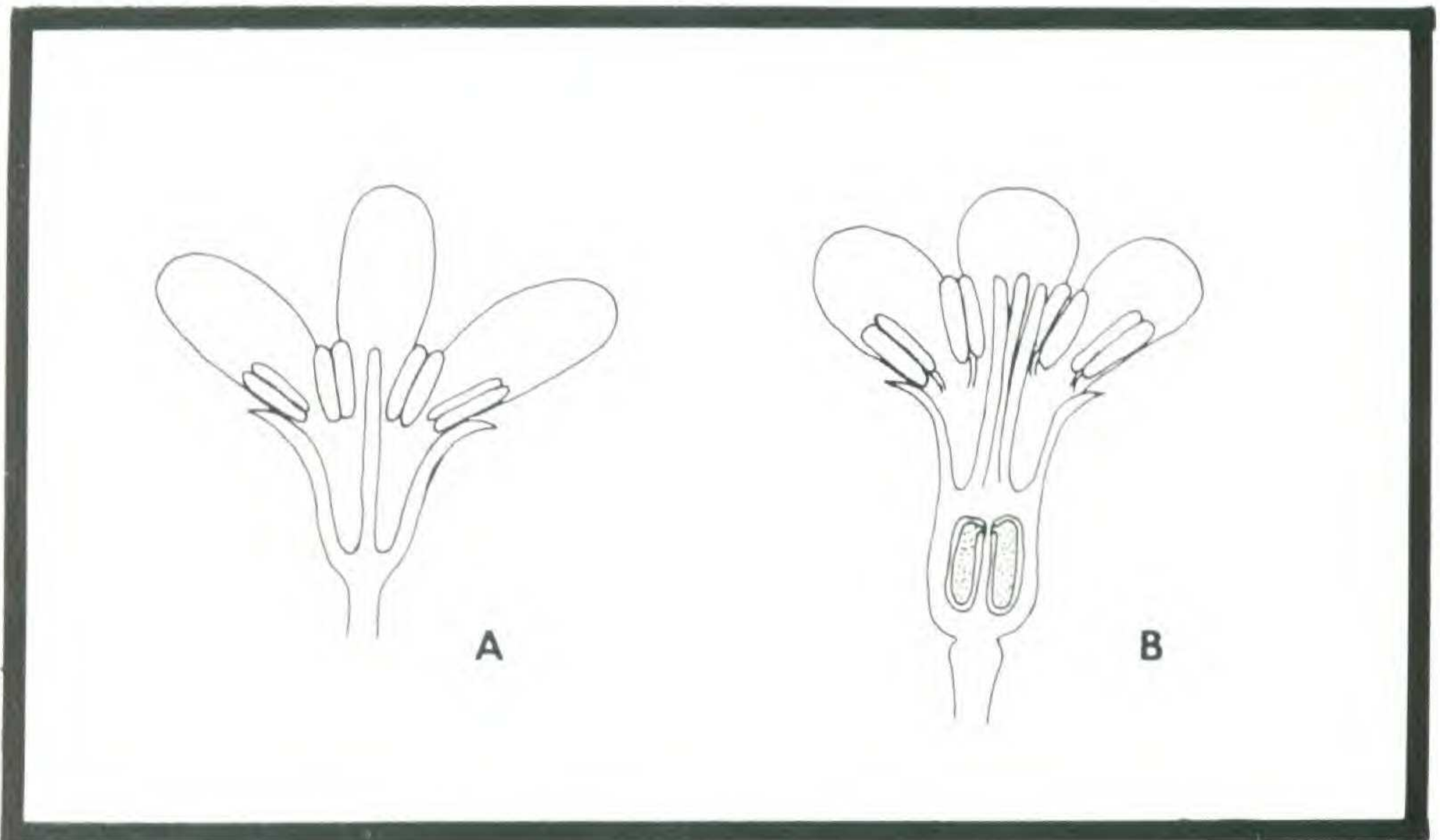


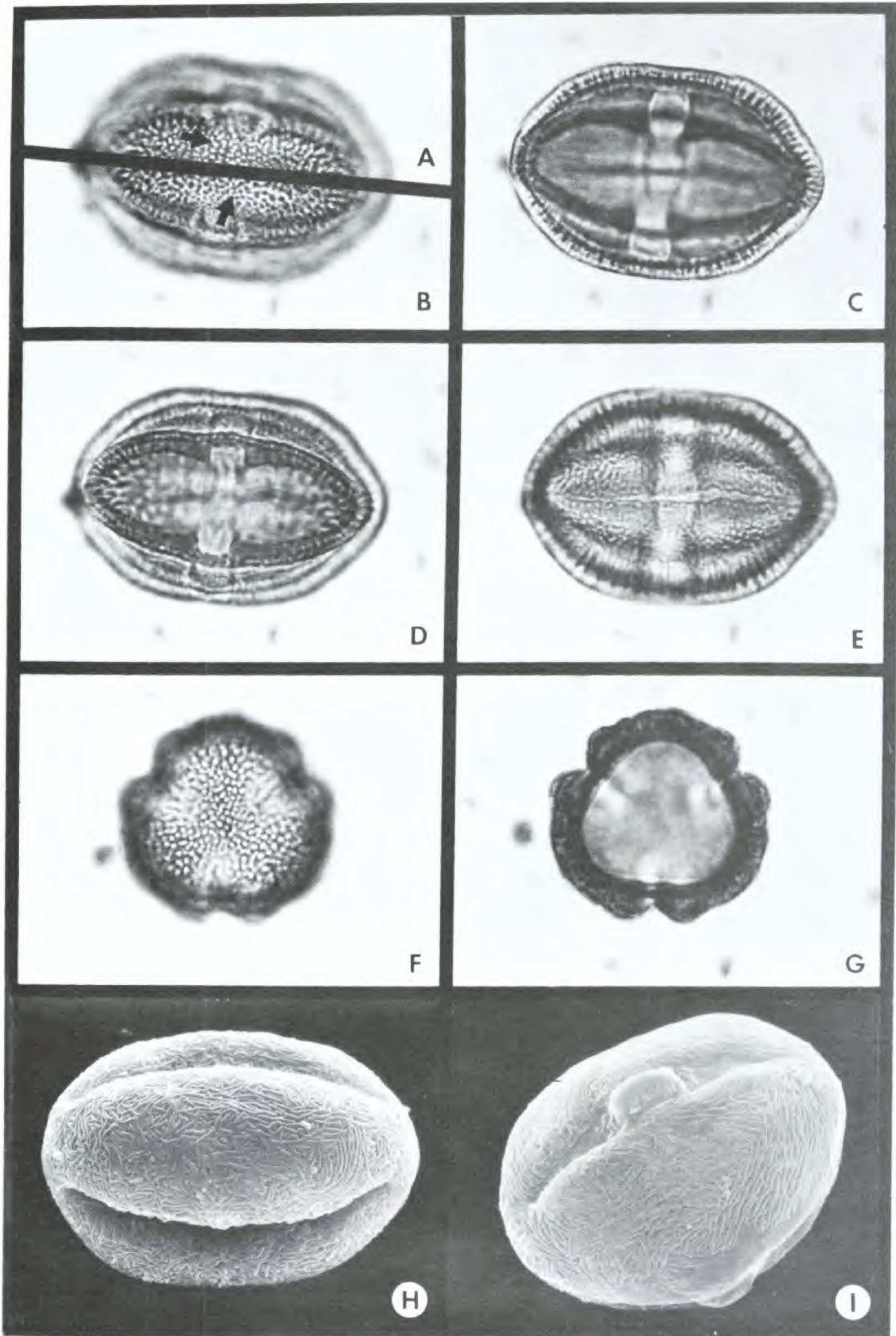
Fig. 1: Two floral types of *Panax trifolium*: A, staminate, B, hermaphrodite.

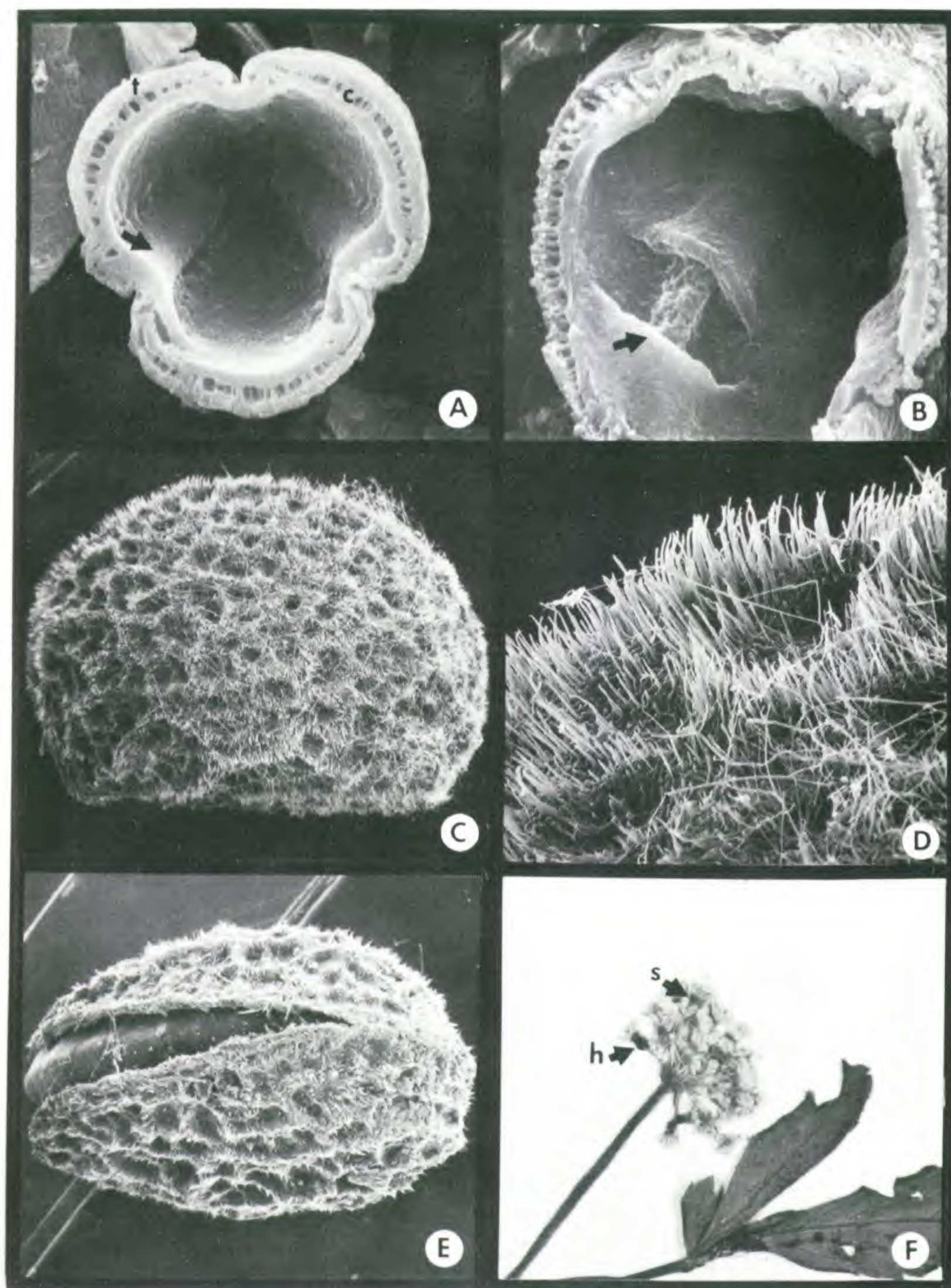
The nexine is approximately  $1\ \mu\text{m}$  in thickness throughout, excluding the previously described poroid regions. The sexine is thicker than the nexine (Fig. 2, C), ranging from about  $2\ \mu\text{m}$  in the center of the equatorial zone to approximately  $3\ \mu\text{m}$  in the central polar area. In both of these locations the sexine becomes thinner toward the colpi.

The sculpturing of the exine is difficult to distinguish through LM analysis alone. Different characters of the exine become apparent when LM observations are compared with those from the SEM. Under LM the grain surface appears reticulate (Fig. 2, A, B, F). SEM micrographs, however, illustrate a distinctly different striate tectum (Fig. 2, H, I; Fig. 3, B). This difference presumably results from a lack of

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Fig. 2: A — E, series of LM micrographs focusing through a single grain in equatorial view. A, high focus showing columellae, appearing white (arrow) ( $1587\times$ ). B, slightly lower focus showing dark columellae (arrow) forming a reticulate appearance ( $1587\times$ ). C, optical cross-section of grain showing thin area of exine in the equatorial region ( $1587\times$ ). D, optical cross-section of poroid areas ( $1587\times$ ). E, surface view showing one colpus and poroid area ( $1587\times$ ). F — G, LM micrographs of grain in polar view. F, high focus showing white columellae ( $1587\times$ ). G, optical cross-section ( $1587\times$ ). H — I, SEM micrographs of separate grains in equatorial view. H, showing two invaginated colpi and the striate nature of the sexine ( $1235\times$ ). I, showing two colpi with slightly protruding colpus membranes in the poroid area ( $1100\times$ ).





relief on the tectum, therefore causing it to appear more or less transparent under LM analysis. This phenomenon is illustrated in Kapp's (1969) LM description for grains of the species in which he reports the sexine to be reticulate. Thus the reticulate appearance is a result of the orientation of the subtending columellae (baculae), not the sculpturing of the tectum itself (Fig. 3, A, B). Very careful LM analysis shows faint striate sculpturing in the peripheral regions of some grains.

No distinct differences in exine sculpturing were found in pollen from the two floral types. However, upon comparison of size measurements some differences were revealed (Table 1). The mean equatorial axis lengths of grains from the two floral types were shown to be similar, but mean polar axis lengths were significantly different. Grains from hermaphroditic flowers exhibited slightly longer polar axis lengths on the average. Also, upon comparison of the ratios of polar to equatorial axis lengths (P/E ratio of Erdtman, 1952) significant differences were again shown (Table 1). Grains from the staminate flowers possessed P/E ratios ranging from 0.97-1.63 (suboblate-prolate) with a mean of 1.30 (subprolate). In comparison those from the hermaphroditic floral form ranged from 1.00-1.70 (prolate spheroidal-prolate) with a mean of 1.45 (prolate).

#### SEED MORPHOLOGY

Seeds of *Panax trifolium* are white and somewhat reniform in shape. The length ranges from 2.5 to 3.5 mm and the width from 1.5 to 2.5 mm (Table 1). The seed coat is characterized by a reticulate network of ridges, from which arise abundant short stiff unicellular hairs (Fig. 3, C, D).

Kapil, et al. (1980) state that seed hairs are usually adaptations for wind dissemination (anemochory), but note that they also function

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Fig. 3: **A — B**, SEM micrographs of sliced open grains. **A**, grain sectioned approximately in the equatorial plane showing the thickening of the nexine along the colpi (arrow), also showing the tectum (t) and columellae (c) (1655×). **B**, grain sectioned obliquely, showing the two separate nexine thickenings (arrow) parallel to each other in the equatorial zone (2330×). **C — E**, SEM micrographs of seeds. **C**, whole seed showing unicellular hairs high-lighting the reticulate pattern (10×). **D**, close-up of the seed coat showing the unicellular hairs (75×). **E**, whole seed showing split seed coat (15×). **F**, LM micrograph showing an andromonoecious inflorescence; staminate flower (m), hermaphrodite flower (h) (1.5×).

Table 1: Data for comparison of characters of staminate and hermaphrodite individuals.

Character	Staminate Plant				Hermaphrodite Plant				F-ratio (ANOVA)
	Range	Mean	S.D.	N=	Range	Mean	S.D.	N=	
No. of flowers per inflorescence	9-41	19.3	7.53	33	3-12	7.1	2.23	33	79.87
Total duration of inflorescence flowering (days)	12-19	14.5	2.46	15	5-8	6.0	1.15	15	97.78
Duration from anthesis to fruit maturation (days)	---	---	---	---	20-24	22.5	1.32	15	---
Pollen measurements;									
Polar axis ( $\mu\text{m}$ )	38-49	43.7	2.61	34	34-49	41.6	3.29	34	7.73
Equatorial axis ( $\mu\text{m}$ )	25-40	31.9	3.83	34	27-38	30.5	2.12	34	3.53
P/E ratio	0.97-1.63	1.30	---	34	1.00-1.70	1.45	---	34	---
No. of grains per anther sac ( $\times 2$ for total no. in anther)	180-253	210	22.40	22	40-243	157	47.00	22	22.57
Percent stainability									
Aniline Blue	---	99.3%	---	3	---	93.9%	---	3	---
Aceto-carmin	---	91.3%	---	3	---	99.7%	---	3	---
Mal Gr. / Ac. Fucs.	---	99.7%	---	3	---	97.3%	---	3	---
Flower size ( $\mu\text{m}$ )	1.0-1.5	1.2	1.75	30	1.5-2.5	1.30	0.25	30	149.76
Seed length ( $\mu\text{m}$ )	---	---	---	---	2.5-3.5	3.05	1.75	30	---



in water (hydrochory) and animal (epizoochory) dispersal. These mechanisms of dispersal do not seem to apply to the seeds of *Panax trifolium*, which fall to the ground and filter into the leaf litter.

Although the seeds of *Panax trifolium* germinate the next spring after they are shed, I have observed that the seed coat actually splits in the late fall (Fig. 3, E) (Table 2), not just before germination in early spring.

#### FLORAL MORPHOLOGY

The staminate flower of *Panax trifolium* (Fig. 1, A) is composed of a subconical floral tube which surrounds a persistent, reduced, solitary style. Five sepals and five petals alternate on the lip of the floral tube. Five two-celled anthers also arise from the margin of the floral tube opposite the sepals.

The hermaphroditic flower (Fig. 1, B) is composed of a cylindrical floral tube fused below to a three-carpellate inferior ovary which is noticeably swollen at its base. Three styles arise from the top of the ovary. Five sepals and five petals alternate on the lip of the floral tube, along with five two-celled anthers located opposite the sepals.

In the majority of cases the inflorescences of *Panax trifolium* are composed of only one or the other floral form: staminate or hermaphrodite. However, a survey of specimens located in several herbaria revealed that occasional andromonoecy exists; both staminate and hermaphroditic flowers on the same plant (Fig. 3, F). In a sample of 753 plant specimens, on approximately 260 sheets, 516 (69%) possessed only staminate flowers, 229 (30%) only hermaphroditic flowers and 8 (1%) had both flower types on the same inflorescence. I have not observed andromonoecious individuals in the field.

#### FLOWERING PATTERNS AND SECONDARY SEX CHARACTERS

Two distinct plant types occur in *Panax trifolium*. One produces morphologically and functionally staminate flowers. These possess a full complement of five anthers as well as a single short style, but lack a noticeable ovary. The other plant type produces morphologically hermaphroditic flowers possessing one three-carpellate ovary, each carpel capable of producing a single seed. These flowers also contain the full five anther complement.

Table 2: **Pollen:ovule ratios; percent seeds with split seed coats; percent seed set; results of bagging.**

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Percent seed set:

Total number of fruits collected: 154 from 22 plants.

Number with full (3/3) seed set 93 (60.4%)

Number with less than full seed set 61 (39.6%)

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Percent seeds with split seed coat:

Date coll.	N=	Number with split seed coat	Number with non-split seed coat
4 Nov. 1981	53	34 (64.2%)	19 (35.8%)
30 Nov. 1981	33	31 (93.9%)	2 (6.1%)
23 Jan. 1981	16	13 (81.3%)	3 (18.7%)

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Pollen:Ovule ratio:

total no. grains per staminate flower

total no. ovules per hermaphrodite flower = 696:1

total no. grains per staminate and hermaphrodite flowers combined

total no. ovules per hermaphrodite flower = 1220:1

mean no. grains per staminate inflor. = 986:1

mean no. ovules per hermaphrodite inflor.

mean no. grains per staminate and hermaphrodite inflor. = 2378:1

mean no. ovules per hermaphrodite inflor.

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Seed set.

	No. seeds set	No. plants observed
Plants left uncovered (control)	25	10
Plants covered	0	15

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Both plant types of *Panax trifolium* bloom concurrently within the population, with floral development and maturation taking place while the inflorescence is in a drooping position. Lloyd and Webb (1977) reported that staminate individuals of a dimorphic species often begin flowering before the seed-producing plant. I have not found this to be the case with *Panax trifolium*.

I have found several distinct differences between the two plant types (Table 3) that have been termed secondary sex characters (Lloyd & Webb, 1977). Distinct size differences of flowers, measured in bud, between the two plant types is obvious (Table 1; Fig. 3, F). This distinction is directly related to the presence of a fully developed ovary in one floral form and not in the other. Differences in numbers of flowers per inflorescence and their pattern of flowering were apparent. Significantly more flowers were observed on staminate inflorescences than on hermaphroditic, averaging 19 and 7 respectively (Table 1). The sequence of flowering of the staminate inflorescence was from the outermost flowers inward (centripetal), in contrast with the hermaphroditic inflorescences in which the flowers all opened more or less simultaneously. As a result of the differences in flowering patterns, the duration of flowering of the respective inflorescences differed markedly. Individual flowers, whether staminate or hermaphrodite, remained open for about four to five days. However, the entire staminate inflorescence blooms about twice as long as the hermaphrodite, averaging about 15 days for the staminate versus 6 for the hermaphrodite (Table 1). On the

Table 3: Secondary sex characters used in comparison of the two plant types.

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- 1) Number of flowers per inflorescence.
  - 2) Total duration of flowering per plant.
  - 3) Sequence of flowering of respective inflorescence.
  - 4) Amount of pollen produced per anther.
  - 5) Percent stainability of pollen.
  - 6) Flower size.
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population scale this prolongs the total time that pollen is available and no doubt plays an important role in the pollination biology of the species.

During anthesis the staminate flower sheds its pollen and the anthers then fall. However, the perianth persists on these spent flowers and the flowers remain attached to the inflorescence until all the flowers have passed. After this time the inflorescence wilts and falls, or the entire stem dies. The persistent perianths may contribute to the attractiveness of the staminate inflorescence, drawing insects to the inner flowers that are still shedding pollen.

Anthesis proceeds very differently in the hermaphroditic flower. As the flowers open the anthers dehisce while the styles remain pressed together. After anther dehiscence, the styles begin to separate, becoming fully divergent after the anthers have fallen (protandry). Occasionally some overlap exists between the time of anther dehiscence and style divergence. The styles remain divergent for three to four days while pollination takes place. After this time they discolor and wilt slightly, after which the perianth is shed.

The significance of simultaneous blooming of the hermaphroditic inflorescence may be related to its protandrous nature. If non-simultaneous flowering occurred, selfing between flowers within an inflorescence (geitonogamy) would be more likely to take place. The simultaneous nature of flowering may increase the probability of outcrossing. At the time of stigma divergence there would be a better chance that all the pollen had been shed and the probability of outcrossing would be increased. Cruden (1977b) reported this same character in protandrous umbelliferous taxa.

The staminate plant often lives for only a few days after anthesis. Due to the fruit development period, the hermaphroditic stem persists well past anthesis. The initiation of fruit development, indicated by ovary expansion, begins very soon after the styles have wilted, often before the entire perianth has fallen. The time from style wilting to fruit maturation and drop averaged 28 days (Table 1). In many cases fruits which lacked the full three seed complement were observed (Table 2). It is not known whether this lack of seed set is related to an insufficient pollen or nutrient supply or to some other factor. Upon maturation the fruit becomes slightly yellow and falls from the plant, a result of an apparent abscission zone at the base of the ovary. On the ground the fruit wall quickly breaks down,

often along the septations between carpels. The seeds then fall from the fruit, sometimes forming small piles where several fruits have fallen together. My observations differed from those of Hu, et al. (1980) where they observed seeds being expelled from the fruits while the latter were still attached to the plant. After the fruits have fallen the stem lives for several more days, turns yellow and dies. Once shed, the seeds filter down into the litter. Germination takes place early the following spring.

Differences also exist between the two floral types regarding the amount of pollen produced per anther; the staminate producing approximately 25% more pollen per anther than the hermaphrodite (Table 1). Although less pollen is produced in the hermaphroditic flowers, that which is produced seems significant in amount and therefore should be considered when assessing pollen flow within the population. The staining qualities of the pollen from the two types also differed somewhat. When stained, pollen from staminate flowers consistently showed a higher staining percentage (less grain abortion), about 100% for staminate and 95% for hermaphroditic (Table 1). I prefer to use the phrase "staining percentage" rather than "viability percentage" because the staining characteristics of pollen are only an estimate of viability, not a definitive test.

Although the observations were not quantified and were somewhat inconsistent, there seemed to be differences in the degree to which the different grains took up the stain: the grains from staminate flowers often stained slightly darker than those from the other floral type. These slight differences could signify fertility differences and are therefore noteworthy.

If the breeding system of *Panax trifolium* is one of functional dioecy, distinct differences between functional versus non-functional pollen produced by the two floral types would be expected. Barrett and Helenurm (1981) reported that the anthers of the functionally female flowers of *Aralia nudicaulis* did not produce pollen, and Bawa (1977) found that anthers in similar functionally female flowers of *Cupania guatemalensis* produced pollen, but that anther dehiscence failed to occur. Anderson and Gensel (1976) and Anderson (1979) reported the lack of aperture development in pollen from what were interpreted as functionally female flowers of a species of *Solanum*. I have not observed any of these phenomena in *P. trifolium* other than the size differences noted earlier in the discussion of pollen morphology.

## POLLINATION AND SEX RATIOS

Although not referring to dimorphic taxa, Cruden (1977a) illustrated a relationship between the ratio of pollen grains to number of ovules in a flower and its pollination mechanism. The more haphazard the mechanism the higher the pollen/ovule (P/O) ratio. This ratio can be estimated variously for *Panax trifolium* (Table 2). However, even in the estimate resulting in the largest ratio (2378.1), this ratio is still relatively small and suggests a rather predictable pollination mechanism. This agrees with the observations of pollinators made throughout this study.

Pollination in the species appears to be primarily entomophilous. Members of the insect families Empididae, Scatopsidae, and Syrphidae (Diptera) were observed visiting, and were collected upon, flowers of *P. trifolium*. Members of the Syrphidae were observed visiting the staminate flowers, where they initially collected pollen from several anthers, cleaned themselves of excess pollen and then reached to the base of the floral tube for an apparent "drink of nectar." This series of events was seen on several occasions and was also observed, but in less detail, on hermaphrodite flowers.

During early morning visits to the populations mosquitos were often seen sitting on flowers of *Panax trifolium* as well as those of *Coptis groenlandica* and *Anemone quinquefolia*. Although mosquitos are known to take part in pollination of some orchids (Stoutamire, 1968, 1971) these insects were never observed visiting the reproductive organs of *P. trifolium* flowers and were presumably only "resting."

A random walk through one population revealed a sex ratio highly skewed to staminate individuals; 110 staminate versus 16 hermaphrodite (approximately 7:1). This, combined with the higher numbers of flowers in staminate versus hermaphrodite inflorescences, indicates a relatively high pollen to ovule ratio at the population level. More detailed investigations into this phenomenon are required before the true significance of this ratio can be appreciated.

As a result of caging experiments in which 15 hermaphroditic plants were covered with nylon screening it was shown that significant anemophily probably does not occur (Table 2). In all cases no fruit development occurred on the covered plants whereas all uncovered plants in the same area exhibited significant seed set. This also

rules out mechanical self pollination but not necessarily self incompatibility.

#### CONCLUSION

The results of these investigations suggest that the pollen produced in the hermaphroditic flower appears functional, although possibly to a lesser extent than that from the strictly staminate flower. This, combined with the protandrous nature of the hermaphrodite flower, suggests that androdioecy may better characterize the breeding systems of *Panax trifolium* than previous designations. However, actual confirmation of androdioecy will not be accomplished until detailed crossing experiments within and between the two plant types are completed.

*Panax trifolium* is unique in that it exhibits ideal characters needed to conduct a survey regarding age structure of staminate and hermaphroditic plants in a population. During the growing season rhizomes of staminate and hermaphrodite individuals can be uncovered and their age determined by counting the persistent leaf scars. This allows a unique opportunity to estimate the longevity of the sexes, usually a very difficult undertaking. During the spring of 1981 a rhizome of *P. trifolium* was excavated which possessed approximately 30 leaf scars on a portion about 4 cm in length. Because one leaf is produced per year the plant was therefore about 30 years old.

The results of this study make a contribution to the current knowledge of several aspects of the reproductive biology of *Panax trifolium*. However, there remain many additional areas of investigation which have yet to be addressed, regarding among others, sex ratios, confirmation of pollen fertilities, self-compatibilities, and population age structure.

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